Methods used to survey avian species and their potential for surveying ground-dwelling birds in Asia

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There is an increasing need for reliable information on bird populations in Asia and several methods have been used for population estimation: some were based on the way that species were detected (e.g. calling or territorial display) in field surveys and others have been developed from an understanding of sampling theory. Many bird species in Asia inhabit areas that are challenging to survey; we consider the basis of some of the more widely used methods in order to assess which are likely to be useful for providing data on populations. We review four methods: 1) spot mapping; 2) triangulation; 3) distance sampling (using line transects and point counts); and 4) camera trap sampling. Four aspects were assessed: What has it been used for? What are the method's assumptions? What field protocol is required? What analytical methods should be used? Spot mapping and triangulation are both based on the ability to detect individuals of the target species in the field, but lack a statistical basis for converting this into a meaningful estimate about the population surveyed. Distance sampling is, in contrast, based on sampling theory and meeting some of the assumptions for detecting individuals in the field can be difficult. Nonetheless, it is increasingly widely used and considered reliable for making estimates about bird populations. Finally, camera trapping is a useful method for rare and cryptic species and the analytical techniques that cover the wide range of contexts in which it may be used are being developed.

INTRODUCTION

Quantitative data on populations (i.e. density or size) of a given species in a specific area are very important for wildlife conservation in a range of different contexts and for varying purposes. Density estimates, for example, provide baseline data on species abundance that can be used to derive population sizes and these can be monitored over time to assess the suitability of conservation strategies (Sutherland *et al.* 2004, Nijman & Menken 2005). Understanding these population changes is very important if policy and management plans are to be based on a sound understanding of species status. Reliable estimates of such population trends require careful design of the sampling strategy and field protocols that are standardised and repeatable with high detection probability and low observer variability (Thompson *et al.* 1998, Yoccoz *et al.* 2001, Pollock *et al.* 2002).

The demand for data to both assess the status of species of conservation concern and to inform the management of those with the highest probability of extinction is most acute in the tropics and subtropics where most threatened vertebrates are thought to occur (Laurance 2007), the knowledge of species ecology is severely limited, and habitat loss and illegal hunting present serious problems for many species (Wright & Muller-Landau 2006). This is compounded by the difficulty in accessing terrain in areas that are mountainous or that have dense forest structure (e.g. tropical rainforest), making it a challenge to relate information about encounter rate (sighting or vocal detections) to populations (abundance, density or size).

There is, therefore, a considerable need to encourage the collection and analysis of data that can be used to inform assessments of species status, wherever this is possible. Yet, for many who have an interest in avian fieldwork and who are keen to gather such data but lack detailed knowledge in survey techniques, determining which method to use and understanding how to use it properly is difficult. This is because of the complexity of different contexts in which each method has been used, the purpose of the study and the various assumptions that have been made when developing the field protocols and in turning the field data into population estimates. Although there is a variety of texts available for surveying birds (e.g. Sutherland 1996, Bibby *et al.* 1998, 2000), a range of studies and developments have taken place since these were published that we seek to reflect here. Furthermore, our aim is to review, briefly, methods that have long been used or considered for birds in the tropics. We seek to present a summary of these methods in a form that will guide potential first-time users towards a method that will best suit their purpose and circumstances. Although we consider Asian birds in general, we place special emphasis on ground-dwelling species such as pheasants, because they are often of high conservation concern (e.g. because of ground-snaring) and can be difficult to detect.

A range of methods have been used to collect data on terrestrial bird populations elsewhere, but their reliability and usefulness have not been reviewed critically and related to the data needs of species in Asia, especially where terrain and habitat are challenging. These methods include those that have been developed because of the way individuals in a species are detected (e.g. spot mapping, triangulation and now camera trapping) and those based on sampling theory (e.g. distance sampling using both point and line transect). All these methods have been used in order to generate population estimates of one sort or another, but there is limited guidance on what methods are suitable in which circumstances (e.g. the purpose of the survey, the ecology of the target species and the terrain and habitat being surveyed). Consequently, we seek to answer the question: what are the options and which should be considered for a particular purpose and context? The aim of this synthesis is to provide a succinct review of the key features of four population estimation methods that have been used in South and South-East Asia, consider their utility for ground-dwelling birds in the region, and provide references to further information. We examine where each method has been used and for what purpose, the field protocol employed, the analytical methods required and their statistical assumptions. We also included gibbons in our review, because their vocalisations show striking parallels with songbirds (Clarke *et al.* 2006), and because they have also been the subject of methodological research in order to estimate population size from the detection of loud calls and sightings; there may therefore be lessons that can be learnt for avian population estimation in the region.

METHODS

We reviewed four methods used to survey birds to provide data that are relevant to monitoring population changes. These methods are: 1) spot mapping (also known as territory mapping); 2) triangulation; 3) distance sampling using both line and point transects; and 4) camera trapping. To ensure that we reviewed a wide representation of appropriate research we conducted a structured search of available literature. Given our aim and objectives, an exhaustive systematic review (*sensu* Collaboration for Environmental Evidence 2013) of avian population estimation was not appropriate, so we tailored our search protocol to maximise efficiency without compromising the range of literature that we reviewed.

We searched three databases for studies that have used these methods in published findings, namely: Google Scholar, Newcastle Library Search and Science Direct. The Newcastle Library Search includes a wide range of resources (see http://www.ncl.ac.uk/library/resources/library-search/) and includes most material in major bibliographic databases and from major journal publishing companies (e.g. Wiley and Elsevier). Searches were conducted using standardised search terms that described the methods and sought to limit the studies identified to those that were taxonomically relevant. For example, searches for spot mapping were undertaken using phrases 'spot mapping' and 'territory mapping' and included taxonomic terms such as 'birds'.

Once relevant papers had been identified we reviewed the papers to extract information that would help us answer four questions: What has it been used for? What are the method's assumptions? What field protocol is required? What analytical methods should be used? Our overall aim was to provide a succinct review of these key features, provide references to further information and to consider how useful these methods are for population estimation of birds in South and South-east Asia.

RESULTS

Table 1 summarises key aspects of each of the methods reviewed and we discuss key aspects of that summary below. Please refer to the table for further details and sources of information.

Table 1. Comparison of spot mapping, triangulation, distance (point and line transect) and camera trap sampling.

	Spot mapping	Triangulation	Distance sampling	Camera trap
Purpose	Density	Density/abundance distribution	Density/encounter rate/distribution	Population/density/abundance Capture rate/species richness Distribution/behaviour/habitat selection
Assumptions	1. Population is closed 2. Species is territorial 3. Species are identified correctly	1. Individual calls every morning 2. Animal groups are independent of each other 3. All individuals/ groups were heard calling from a station	1. Individuals on the line or point are always detected 2. Individuals do not move 3. Measurements are exact	*Capture–recapture*: 1. Population is constant during study 2. The sample is random 3. Capture probability of each individual > zero *Presence-absence/repeat count*: 1. Detection is independent 2. Detection probability of individual is constant over time
Field effort	5–10 consecutive visits	3–5 (gibbons) or 1–4 (Galliformes) consecutive days	3–5 consecutive days	10–60 trap day/night
Sampling	Study area divided into a grid, quadrats, points or strip transects, for intensive surveys	Listening posts established at vantage points and distance and bearing of calls heard are recorded	Point transect: Random or stratified across study area and points with variable radius Line transect: Random or stratified across study area and transects with variable distance	Camera traps should be set to maximise the chances of detecting target species and the distance between camera traps must be smaller than territory of target species
Analysis of data	Most widely used formula is: density (pairs or territories/ha) = number of mapped territories/pairs mapped divided by size of area (in ha) surveyed See (B) below for examples of studies	Gibbon densities have been estimated following Brockelman & Ali (1987) and Brockelman & Srikosamatara (1993). Population indices for Galliformes follow Gaston (1979) See (C) below for examples of studies	The software programme Distance is widely used, but Bayesian approaches (Eguchi & Gerrogette 2009, Amundson *et al.* 2014), PAST Program version 2.05 (Jolli & Paddit 2011), and Distance Package in R Program (Kidwai 2013) are also used See (D) below for examples of studies	A range of analytical techniques are used, depending on the study See (A) below See (E) below for examples of studies
Requirements	Identification of species by sight and song/call	Identification of species by sight and song/call and estimation of distance	Identification of species by sight and song/call and estimation of distance	Skill to select camera location and set traps appropriately
Used for	Breeding and territorial birds	Gibbons Galliformes	Point transect: songbirds Line transect: wide range of taxa	Terrestrial birds and mammals

(A): The following analytical techniques have been used to calculate abundance and density, depending on context (see text): 1) capture–recapture using CAPTURE; 2) mark–resight–capture using MARK and R package Software Program; 3) photographic rate; 4) occupancy/presence–absence/repeat count using Presence, MARK software program; 5) spatially explicit capture–recapture (SECR) using DENSITY program, R package SECR, Bayesian framework in WinBUGS, R package SPACECAP software program.

(B): Examples of studies using spot mapping for estimating the density of songbirds include Best (1975), Jones *et al.* (2000), Tomiałojć (2004) and Yoon (2010). Examples comparing the accuracy of field survey methods include Tarvin *et al.* (1998), Howell *et al.* (2004), Bocca *et al.* (2007), Gale *et al.* (2009), Gottschalk & Huettmann (2011), Greene & Pryde (2012) and Newell *et al.* (2013).

(C): Examples of studies using triangulation for estimating gibbon densities include O'Brien *et al.* (2004), Nijman & Menken (2005), Aldrich *et al.* (2006), Jiang *et al.* (2006), Hamard *et al.* (2010), Luu Quang Vinh *et al.* (2010), Phoonjampa *et al.* (2011), Höing *et al.* (2013), Timmins & Duckworth (2013) and Thongbue *et al.* (2014). Examples estimating the abundance and distribution (presence–absence) of loud-calling Galliformes include Garson (1998), Baral *et al.* (2001), Kaul & Shakya (2001), Jolli & Pandit (2011) and Sailo *et al.* (2013). Examples estimating the density of Galliformes include Gaston *et al.* (1980), Mahato *et al.* (2006), Poudyal *et al.* (2009) and Jain & Rana (2013).

(D): Distance sampling has been used for a wide range of purposes across a range of species and habitats. These include estimating densities of breeding birds (Jarvinen & Väisänen 1975), moorland passerines (Thirgood *et al.* 1995), Cracidae (Begazo & Bodmer 1998), migrating birds in forest wetlands (Wilson *et al.* 2000), monitoring seabirds (Certain & Bretagnolle 2008) and studying cetaceans (Hammonda *et al.* 2013). Examples of studies estimating the density and abundance of Galliformes in Asia include Azhar *et al.* (2008), Jolli & Pandit (2011), Kidwai *et al.* (2011), Ramesh *et al.* (2011), Selvan & Sridharan (2012), Kidwai (2013) and Selvan *et al.* (2013). See also Warren & Baines (2011); studies of encounter rate include Wang *et al.* (2004) and Ashraf *et al.* (2005) and of distribution include Lalthanzara *et al.* (2014).

(E): Studies using camera traps to sample populations include: various studies on cat populations, Karanth (1995), Karanth & Nichols (1998), Carbone *et al.* (2001), Azlan & Sharma (2003), Silver *et al.* (2004), Karanth *et al.* (2006), Soilaso & Cavalcanti (2006), Harmsen *et al.* (2010), Tempa *et al.* (2011) and Lynam *et al.* (2013); ungulates, Rovero & Marshall (2009) and Asian tapir, Linkie *et al.* (2013). Studies assessing species richness and community composition include Silveira *et al.* (2003), Bernard *et al.* (2013) and Liu *et al.* (2013), and monitoring the status and trend of tropical rainforest terrestrial vertebrates include Ahumada *et al.* (2013). Studies using camera trapping to study bird species in Asia include Winarni *et al.* (2009), Li *et al.* (2010) and Samejima *et al.* (2012).

Spot mapping or territory mapping

Spot mapping was first proposed by Williams (1936) and has been commonly used for intensive surveys to estimate abundance and density of territorial and singing birds in a relatively small area. It has largely been used in the temperate habitats of Europe, North America and New Zealand (e.g. Best 1975, O'Brien *et al.* 2004, Yoon 2010) and only rarely in the tropics (e.g. Thiollay 1994, Stouffer 2007, Gale *et al.* 2009, Peel *et al.* 2015). It has also been used to test the effectiveness of other survey methods such as point counts (Howell *et al.* 2004), radio-telemetry (Bocca *et al.* 2007), mark–resighting (Greene & Pryde 2012) and, in South-East Asia, distance sampling (Gale *et al.* 2009) and camera trapping (Suwanrat *et al.* 2015).

Spot mapping can both overestimate (Enemar *et al.* 1979, Cyr *et al.* 1995) and underestimate population size (Snow 1965, Bell *et al.* 1973, Nilsson 1977, Paul & Roth 1983, Streby & Loegering 2012) depending on the detectability of the focal species, the census period (Enemar *et al.* 1979), the ability of the observer (O'Connor & Marchant 1981), the territorial behaviour of the species (Best 1975, Enemar *et al.* 1979, Bocca *et al.* 2007) and sample size (Enemar *et al.* 1978).

Assumptions

Turning field data into meaningful population estimates requires that: 1) populations are stable during the time of study and that animals remain in their territories during sampling periods; 2) animals are correctly identified to species; 3) territory owners are sufficiently conspicuous to be recorded on successive visits; 4) observers do not differ in their ability to detect animals (Ministry of Environment 1999). In Asian forests, it is rarely possible to detect a large enough proportion of individuals in the study area for this method to be appropriate.

Field protocol

Spot mapping is used during the breeding season for species that are defending territories using conspicuous behaviours (e.g. song, visual displays) and can, therefore, be detected easily, or with animals that have been marked. Study areas may be about 2–4 km^2, which are then subdivided to sample units in the shape of a grid, quadrats, points or strip transects for intensive surveys. Ideally, data are collected simultaneously by two or more observers and then combined to produce a map containing all detections of the species's territories. Observers should cover every part of the study area several times, and it has been suggested that each sample unit requires at least 7–10 visits that should be made during periods of peak activity (typically in the morning and in the afternoon/evening). Surveys should be conducted during good weather conditions (Best 1975, Enemar *et al.* 1979, Tarvin *et al.* 1998, Howell *et al.* 2004, Tomiałojć 2004, Greene & Pryde 2012).

Analysis

The locations where the focal species is recorded from all observers are combined and mapped, and the spatial pattern of records (e.g. clustering) is used to determine where territories are positioned. This can be done in two ways: 1) each observer interprets territorial boundaries by themselves and then an average is taken of the number of territories that each observer has identified; or 2) a single map is produced by an experienced observer. The estimate of territory density can then be calculated by dividing the number of territories mapped by the size of the area surveyed to give the number of pairs or territories per hectare or km^2.

Recommendations for surveying ground-dwelling birds in Asia

The advantage of using spot mapping is that the method can provide accurate monitoring of populations of territorial species in a fairly small area. It is more problematic, and unlikely to be useful, where the area to be surveyed is large and access is difficult, such as rugged terrain where access is only via ridges or where there are large tracts of dense habitats that are difficult to navigate. Spot mapping requires a high level of observer skill in identifying and documenting bird species reliably and the field protocol is time consuming. It can be difficult to use in dense habitat (if sightings are a principal method of detection) or where bird densities are high (Gregory *et al.* 2004). Ultimately, it is likely to be useful for ground-dwelling species in very few cases.

Triangulation or fixed point count or call count

Triangulation was developed for gibbons by Brockelman & Ali (1987) as a way of surveying these territorial and loud calling species. It has subsequently been used to estimate the number of gibbon groups, where the social structure and calling behaviour allow specific assumptions to be made that provide density or abundance estimates (e.g. Nijman 2001, Phoonjampa & Brockleman 2008). Some bird species in Asia, especially pheasants in the Himalayas, have also been counted by plotting on a map ('triangulating') calls that have been detected by at least two or more observers at the same time from fixed points that are an appropriate distance apart. This method has been used to assess the distribution and status of species such as Western Tragopan *Tragopan melanocephalus*, Himalayan Monal *Lophophorus impejanus*, Cheer Pheasant *Catreus wallichi* and Koklass Pheasant *Pucrasia macrolopha* in the Himalayas of India, Nepal and Pakistan (Gaston *et al.* 1980), and for species such as Indian Peafowl *Pavo cristatus* in lower elevation areas of India (Jain & Rana 2013).

Assumptions

Turning field data into a population estimate requires that: 1) each individual (or individual in a group, if a group is the unit being surveyed) calls at least once during the study period (Nijman 2001); and 2) listening posts are selected with the assumption that all groups calling could be heard (Jiang *et al.* 2006, Awan *et al.* 2014).

Field protocol

Vantage points are selected so that calls can be heard from as wide an area as possible, such as on top of a ridge or where both sides of a valley can be monitored, and calls of target species are located from these points (Gaston 1979). The spacing of listening posts depends on the distance from which the target species can be heard. For example, it is often assumed that all pheasants within 400 m can be heard, although some researchers use a fixed radius of 300 m (e.g. Jolli & Pandit 2011, Awan *et al.* 2014), hence observers should be stationed accordingly. Mapping all calls by measuring the compass bearing and estimating the distance from the observer permits duplicate records to be eliminated and may show clusters of records that correspond to the home ranges of particular individuals.

Analysis

The population size, density and abundance index of a target species in an area can be estimated based on the number of individuals/groups recorded calling. This is done as follows: 1) the population of calling birds in an area = the number of the species counted in the survey area multiplied by [total area/census area], with the condition that survey area must be more than quarter of the total study area; 2) density index = maximum number of individuals heard calling in the area divided by the survey area covered by all stations; and 3) abundance index is either a) = number of calling birds heard divided by time spent to survey, expressed as birds/100 hours, or b) = number of calling birds heard divided by number of stations from which birds were detected or distance between survey stations, expressed as birds/station or kilometre (Gaston 1979).

Recommendations for surveying ground-dwelling birds in Asia

This method was developed because it could be used for loud-calling and territorial species over a large area in a short time span and was particularly suitable in rugged or difficult terrain. It was first used for Himalayan Galliformes at a time when there was limited statistical underpinning of population estimation and allowed measurements to be made and understood. As our knowledge of the statistical assumptions required to permit reliable measures develops and the degree to which the ecology and behaviour of the target species meets those assumptions is uncertain, there are questions about the usefulness of this method without greater statistical underpinning. For example, caution is required when translating numbers heard into population measurements, unless it is known what proportion of the population tends to call (e.g. all males and females or all males and no females or only some males). Understanding social behaviour of gibbons has allowed the method to be applied in some contexts in Thailand. Overall, there is currently insufficient understanding of social and calling behaviour of Asian birds to allow detections to be translated reliably into population estimates.

Distance sampling

Distance sampling, using both line and point transects (see *Field protocols* below), is based on the distance between the observer and the animal. Distances to observed animals are measured as the perpendicular distance from the line transect or as the radial distance from a point transect. The method allows calculation of a detection function, as the likelihood of detecting the species decreases with increasing distance from the line or point (Buckland *et al.* 1993, Thomas *et al.* 2010).

Assumptions

Recent advances in distance sampling (Buckland *et al.* 2001, 2008, Laake & Borchers 2004, Thomas *et al.* 2010), have allowed some of the original assumptions to be relaxed, leaving three main key assumptions: 1) individuals on the line or point are detected with certainty; 2) individuals do not move; and 3) measurements are exact—this is a key issue for aural detection in dense habitat as measuring distances precisely is extremely difficult. To address this, Gale *et al.* (2009), working in Thai forest, suggest grouping records together in intervals (e.g. 5, 10, 15, 20, 25, 30, 40, 60, 80 and 100 m) to reduce error. This can be done in two ways: 1) assigning records to intervals during fieldwork, which is complicated when conducting line transects by the need to calculate the perpendicular distance to the transect line; 2) recording ungrouped data in the the field and then grouping it prior to analysis (Buckland *et al.* 1993).

Field protocols

There are two principal field protocols for gathering distance sampling data: line and point transects. Line transects can have either variable length or width or a fixed width or length (strip transect) (Begazo & Bodmer 1998, Bernardo *et al.* 2011). An observer walks along the line transect and records each individual of the target species by estimating the perpendicular (i.e. shortest) distance from the individual to the transect line (i.e. not the distance from the individual to the observer). Point transects are counts from points (rather than walking along transect) and may have a variable or fixed radius and a fixed time for recording. These are likely to depend on the species surveyed (Tarvin *et al.* 1998, Marsden 1999, Norvel *et al.* 2003, Howell *et al.* 2004). A thorough assessment of field protocols and distance sampling's underlying assumptions has been carried out on Philippine forest birds by Lee & Marsden (2008). Marsden (1999) explored the use of point counts for estimating hornbill abundance on Buru and Seram, Indonesia.

Analysis

The first step in the analysis of distance sampling is modelling the probability of detection as a function of distance from the point/transect. This assumes that all individuals at zero distance (i.e. on the line or point) are detected and that detectability usually decreases with increasing distance from the line or point (Buckland 1993, Thomas *et al.* 2010). Most distance sampling analyses use the standard DISTANCE software (Buckland *et al.* 1993, 2001, Thomas *et al.* 2010) which can provide density estimates from both line and point transect data. Other software can also be used, such as the Bayesian approach to line transect analysis (Eguchi & Gerrodette 2009), Bayesian software for imperfect detection (Amundson *et al.* 2014) and the PAST software version 2.05 (Jolli & Pandit 2011). Encounter rates can also be determined for an estimate of relative abundance (Ashraf *et al.* 2005, Wang *et al.* 2004). There is also a wide range of ways in which the data can be examined and the analytical process can be manipulated so that it best matches the data gathered.

Recommendations for surveying ground-dwelling birds in Asia

Distance sampling, using both line transects and point counts, is now recognised as the standard method for estimating density and determining the probability of detection (i.e. the likelihood that an individual will be detected if it is present). However, this method typically requires a sample size of at least 60–80 detections for a robust model (Buckland 1993). It is being increasingly used in Asia, and in consequence developments have been required to ensure that detection patterns of target bird species do not violate the method's critical assumptions (e.g. Gale *et al.* 2009, Lee & Marsden 2008, Marsden 1999). Nonetheless, as there is a clear analytical protocol for converting encounters (=detections) into population estimates, this method should be considered for surveying ground-dwelling birds in Asia.

Line transects are suitable for sampling large areas of relatively open homogeneous habitat and species that are easy to detect, large or conspicuous and not especially mobile. It may not be particularly suitable for highly mobile species because of the risk of double counting, whereby one individual may be counted two or more times during one transect or count (Buckland *et al.* 1993, Buckland 2006, Buckland *et al.* 2008, Greene 2012). They are useful for monitoring populations of birds that occur at low densities and they generate more detections than point transects. Line transect estimates tend to have lower bias and higher precision (Buckland 2006, Gale *et al.* 2009).

Point transects are suitable for patchy, dense vegetation and difficult terrain. The field protocol is sufficient to describe basic biological patterns and is suitable for common forest species and those occurring at high density, especially in species-rich habitats where the observer can concentrate on detecting and identifying each species. It is convenient and easier for observers who have no previous experience. Disadvantages include the risk of flushing a target species as the observer approaches a point transect, and much time can be lost travelling between points, which is not efficient for low density species or for monitoring rare birds. It is not suitable for large multi-species groups or situations where there is a high density of individuals at the transect point. It is more sensitive to sampling error because the area sampled by a point transect is calculated using distance from observer to animal directly whereas for line transect it is calculated using the perpendicular distance. However, it is possible to reduce error in measurement distance by grouping data into intervals or categories (Jarvinen & Väisänen 1975, Buckland *et al.* 1993, Buckland 2006, Buckland *et al.* 2008, Thomas *et al.* 2010, Hartley & Greene 2012).

Camera trapping

In the 1880s, George Shira was the first to develop a method using a trip wire and flash system in which a wild animal photographed itself (Kucera & Barrett 2011). Camera trapping is now seen as a method for studying rare and highly cryptic species and has been used to assess species richness, community composition, activity pattern, habitat selection, abundance and density. Karanth (1995) first used cameras to estimate tiger density in India, a species in which individuals can be identified by their stripe pattern. This was followed by the development of a sampling design to estimate tiger population size and density across the country (Karanth & Nichols 1998). Subsequently, camera trapping has developed to allow population estimation of species in which individuals cannot be recognised individually (see e.g. Rowcliffe *et al.* 2008, Samejima *et al.* 2012) and for an Asian pheasant (Suwanrat *et al.* 2015).

Assumptions

There are two main population estimation techniques that use camera trap data and each has assumptions. The first, which relies on the identification of individuals of the target species, uses capture–recapture and requires that: 1) the population size is constant during the sampling period; 2) sampling is random; and 3) every individual in the population has a capture probability greater than zero (Harmsen *et al.* 2010). The second method, which does not need individual identification, is repeated presence–absence and repeated count survey and requires that: 1) animal detections are independent; 2) the population is closed (i.e. the number of individuals in the study area is assumed to be constant across surveys); and 3) the detection probability of a single animal is assumed to be constant across time (Royle & Nichols 2003, Royle 2004). Estimating the trapping rate for populations where members cannot be identified as individuals requires that: 1) animals conform adequately to the model used to describe the detection process; 2) photographs represent independent contacts between animal and camera trap; and 3) the population is closed (Rowcliffe *et al.* 2008, Foster & Harmsen 2012).

Field protocol

Camera traps should be set in an area by dividing it into a grid and selecting a representative position which maximises the chances of detecting the target species. The distance between camera trap locations must be smaller than the territory size of the target species to avoid 'holes' between camera traps (O'Connell *et al.* 2011, Foster & Harmsen 2012). However, for species that cannot be identified individually, it is essential to ensure that the same individual is not detected in two adjacent camera traps and this is done by determining a time interval (e.g. 1 hour) after which it is assumed that the records are of different individuals (Suwanrat 2015). Camera traps are generally left in the study area for 10–60 days. Some camera trap studies use bait and/or scent lures to attract target species to increase the chances of their detection (Rovero *et al.* 2000); however, this has consequences for the calculation of detection probability and estimate of population or occupancy.

Analysis

Population estimation using camera trap data may involve one of five methods. First, capture–recapture (CR), where every individual in a sample can be identified using unique natural markers to estimate abundance (Foster & Harmsen 2012). It can be calculated in software packages such as CAPTURE (Rexstad & Burnham 1992), the closed capture model in MARK (available to download from http://www.phidot.org/software/mark) or using the Rcapture Package in R (Rivest & Baillargeon 2015). Second, capture–mark–recapture or capture–mark–resight, which is a method that does not require that all animals in the sample are marked. It estimates abundance using the frequency of marked and unmarked individuals and can also be performed in software packages such as mark–resight model in MARK and mra Package in R (McDonald *et al.* 2015), This method does, however, require that the number of marked animals is known and so a sample of the population must be captured and marked prior to camera trapping (Foster & Harmsen 2012). The third method is assessment of the photographic rate (= capture rate), which does not require the recognition of individuals to provide a density estimate. This models the process of contact between animal and camera trap (Rovero & Marshell 2009, Foster & Harmsen 2012) and is most effective for species that are relatively wide-ranging (≥1 km/day), although it is necessary to know the speed at which the animal moves. It is not suitable for territorial species or where the area to be sampled is small (Rowcliffe *et al.* 2008). Fourth, occupancy/repeated presence–absence/repeated counts for species can be used where individuals cannot be identified. This analysis can be conducted using PRESENCE (Mackenzie *et al.* 2002, Royle & Nichols 2003, Royle 2004) or MARK. Finally, spatially explicit capture–recapture (SECR) models, which do not require the intermediate step of estimating an effective trapping area. These models have advantages over traditional capture–recapture models and can be conducted in a range of programmes (Tobler & Powell 2013). Animals are assumed to be distributed independently in space to occupy home ranges. It can be used to provide density estimates using Program DENSITY (available for download from http://www.otago.ac.nz/density/) or SECR Package in R (Efford 2016).

After the abundance has been calculated, the density can be determined when the effective sample area is known. This can be done in two ways: 1) half of the mean maximum distance moved by individuals between camera traps for those captured more than once ['mean maximum distance moved' or MMDM]; and 2) half of the diameter of an average animal's home range (O'Connell *et al.* 2011, Foster & Harmsen 2012).

Recommendations for surveying ground-dwelling birds in Asia

Camera trapping involves little disturbance to wildlife once cameras are set and allows detection of ground-dwelling birds that are otherwise found very rarely. Skill is required to select the location for the cameras and then to set them to maximise the likelihood of detections, depending on the target species. Camera trap sampling offers many exciting prospects for field surveys with a range of purposes, such as presence–absence, species richness and population size (abundance and density) in an area. It is being increasingly used in Asia, usually for ground-dwelling species (e.g. Samejima *et al.* 2012, Li *et al.* 2010, Winarni *et al.* 2009)

Appropriate analytical methods for the estimation of density are, however, still being developed and evaluated, as discussed above, and challenges remain. For example, capture–mark–recapture based on the frequency of marked and unmarked individuals requires knowledge of the number of marked animals prior to camera trapping (Foster & Harmen 2012) and assessment of the rate at which a species is captured on cameras (where individuals cannot be identified) requires the description and calibration of the relationship between capture rate and density (Carbone *et al.* 2001, Rowcliffe *et al.* 2008, 2013, Foster & Harmsen 2012). Although challenges remain, analytical progress is rapid.

CONCLUSION

Each method we have reviewed has benefits for one group of species or another. Two methods are based on ease of detection of individuals in the target species (spot mapping and triangulation) and their application to species in Asia requires careful assessment of the robustness of the assumptions behind the analysis. Both distance sampling methods are derived from a clear analytical framework that translates field encounters into a reliable assessment of density. They are based on explicit analytical assumptions and recent advances that address some of the more difficult-to-satisfy assumptions mean that these methods can now be used in more challenging field conditions than previously. The final method, camera trapping, is based partly on technology that allows the detection of individuals in species that have long been very difficult to detect in adequate numbers for any sort of population estimation. Methods for translating these encounters into population estimates are developing rapidly and are more robust for some species than others.

This review of methods may be used as a baseline for considering what field method might be used to make a population estimate of a bird species that either has characteristics that make it difficult to detect or it occupies challenging terrain or habitat, such as mountains or tropical rainforest. Whilst the specific requirements for any study will depend on, amongst other factors, consideration of the detection characteristics of the target species, the terrain and habitat, and the question(s) being asked, some generalities can be drawn.

Distance sampling (line transect or point transect) appears the most suitable method for species that can be detected (by sight or call) at a close distance, and species that can be found at fixed locations (such as display scrapes or dancing grounds) and do not move much or move slowly (e.g. Grey Peacock Pheasant *Polyplectron bicalcaratum* and Hainan Peacock Pheasant *P. katsumatae*).

Population estimates of species that are difficult to detect because they do not call or are visually cryptic and are mobile and those where individuals can be recognised are best made using camera trapping and capture–recapture techniques for abundance and then estimating density. For mobile, cryptic species that are not individually identifiable the most suitable field method is also camera trapping, but the analytical procedure would be different.

Finally, although there is no formal statistical procedure for making population estimates using spot mapping, this can still be valuable in appropriate contexts. These include where the target species is territorial, with appropriate conspicuous behaviour that can be detected easily, and the sample area is compact and can be easily traversed.

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